❶ What are functional types and how should we seek them?

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Introduction

In recent years ecologists have placed increasing emphasis on the use of non-phylogenetic classifications of organisms when describing the structure and functioning of ecosystems. Some (e.g. Heal & Grime 1991) feel that 'classical taxonomy will have to give way to functional classifications'. Hawkins & MacMahon (1989) and Simberloff & Dayan (1991) have reviewed the increasing body of literature on functional classifications and their wide-ranging and often confusing use in ecology.

GCTE has adopted the concept of a functional classification of organisms as a fundamental part of its operational plan. It concluded that

> It will not be feasible to develop models for every ecosystem of the globe nor represent every species within those ecosystems. Thus, the concept that the complexity of the models can be reduced by treating a smaller number of 'functional types' (FTs) is central to the work of Focus 2; it has often been argued that the essential dynamics of ecosystems can be captured by grouping species into a limited number of FTs. (Steffen et al. 1992).

Thus GCTE is committed to the use of functional types*, yet it is not clear what functional types are and how we should seek them.

Here, we briefly review past work related to functional types, concentrating on those issues most relevant to the objectives of GCTE. We examine the various definitions put forward, discuss how functional types might be identified, and ask what success there has been to date in seeking them. Finally we discuss the successes and failures in the application of functional classifications and the issues relevant to GCTE.

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* Throughout this paper we use the terms functional type and functional group synonymously. We do not know of any authors who make a clear distinction between the terms 'group' and 'type'. We have used the term used by authors when closely quoting their work and the most appropriate term in other situations.

Definitions

Although the idea of functional classification can be traced back at least to Theophrastus (about 300 BC), the modern debate really goes back to suggestions made in the 1960s. Root (1967) introduced the ecological concept of *guilds*, defining them as 'a group of species that exploit the same class of environmental resources in a similar way' or species 'that overlap significantly in their niche requirements'. Cummins (1974) discussed a *functional grouping* of organisms in which he wanted '. . . to stress important process-oriented ecological questions'. Botkin (1975) suggested that species can be grouped into a much smaller number of functional types and that these new groupings would 'still allow consideration of the important population interactions'. Related terms are *character* [or adaptive] *syndromes* to describe certain characters that cannot be decoupled because they contribute to a common functional role (e.g. Swaine & Whitmore 1988) and sometimes may have a common phylogenetic origin (Stebbins 1974), and *strategy* as used by Grime *et al.* (1988) to define 'a grouping of similar or analogous genetic characteristics which re-occurs widely amongst species or populations and causes them to exhibit similar ecology'. Paine (1980) used the term *modules* to define groups of closely interacting species.

In addition, functional types have often been described as those biotic components of ecosystems that perform the same function or set of functions within the ecosystem. Friedel *et al.* (1988) defined them as groups that respond similarly to the same perturbation. Noble (1989) discussed a classification based on a set of physiological, reproductive and life history characters where variation in each character has specific ecologically predictive (rather than descriptive) value. Keddy (1992) stated that species can be aggregated into [functional] groups sharing similar traits.

Other terms have been introduced as extensions of the guild concept. Jaksic (1981) highlighted the confusion over the use of the term guild pointing out that some are based on taxonomic classification (*assemblage guilds*) and others on the use of the same resource (*community guilds*). Verner (1984) defined *management guilds* as a group of species that respond in a similar way to a variety of changes likely to affect their environment. Szaro (1986) used the term *functional guilds* with essentially the same meaning as Root's guilds, and, in addition, introduced two more terms: *structural guilds* for a group of species that use the same resource, although not necessarily in the same manner or for the same purpose, and *response guilds* for species that respond in a similar manner to a habitat perturbation. Menge *et al.* (1986) described the same dichotomy as Szaro's structural and response guilds but called them guilds and functional types.

Various subdivisions and amalgamations of basic guild concepts have been proposed. Faber (1991) suggested the use of the term *league* to describe a group of organisms that use more than one resource in a similar way. The need for such a term depends on one's definition of a 'resource'. Walker (1992) described functional groups as the result of further subdividing guilds based on functional attributes. Barbault *et al.* (1991) argued that functional types should be defined in terms of morphology and physiology 'particularly as these properties relate to resources and species interactions' and thus represent 'feeding guilds' or 'plant growth forms'. They defined functionally similar taxa within a functional type to be *functional analogues*. Yodzis (1982) used the term *clique* to describe a set of species that have some food resource in common (although they do not have to use it in a similar way) and a *dominant clique* to describe a clique that is contained in no other clique. Thus each guild in Root's sense is a clique, but a dominant clique may include more species than a guild or even several guilds. Yodzis suggested that a dominant clique may be called a *trophic guild*. Bahr (1982) also suggested higher-order categories called an *ecological sector* for 'broad trophic groups of organisms in common vertical habitat zones' and *ecological species* for groups defined by a binomial consisting of the ecological sector they occupy and their guild. Swaine & Whitmore (1988) also used the term *ecological species groups*, but to refer to groupings similar to Szaro's (1986) response guilds.

In summary, we see several common ideas in the various definitions of guilds and functional types. The main differences are that in one set of ideas, the species can be grouped on the basis that they use the same resource (i.e. *guilds*) and in others by their response to a specified perturbation. The ideas can be further subdivided according to whether the species use the shared resource in the same way, or respond to the perturbation by the same mechanism. We might expect that a group of species that use resources, or respond to disturbances, by similar mechanisms might behave similarly under a range of circumstances and perturbations, and that the classification would have greater extrapolative power. We present a summary of the definitions and suggested names in Tables 1.1 and 1.2 along with the terminology of other authors.

It will be difficult to achieve an agreed and precise definition of a functional group given the wide range of ways the term has been, and probably will continue to be, used. However, we suggest that its use should be confined to groupings based on the response of organisms to perturbations. Thus, a functional group is a non-phylogenetic classification leading to a grouping of organisms that respond in a similar way to a syndrome of environmental factors. Used in this way, a functional group is the basis for

Table 1.1 *Differences between guilds, response groups and functional groups*

	Resource use		Response to perturbation	
	same resource	same way	same response	same mechanism
Structural guild	Yes	No	—	—
Functional (cf. Root) guild	Yes	Yes	—	—
Response group	—	—	Yes	No
Functional group	—	—	Yes	Yes

Table 1.2 *A comparison of the definitions given by various workers*

We have used the best match to our definition from their definitions. Asterisks indicate cases where we know the match is poor.

Authors	Term used	Authors	Term used
our term	**Structural guild**	*our term*	**Response group**
Szaro (1986)	structural guild	Verner (1984)	management guild
Menge et al. (1986)	guild	Szaro (1986)	response guild
Yodzis (1982)*	clique	Friedel et al. (1988)	functional group
		Swaine & Whitmore (1988)	ecological species group
our term	**Functional guild**	*our term*	**Functional group**
Root (1967)	guild	Noble (1989)	functional type
Szaro (1986)	functional guild		
Menge et al. (1986)	functional type		
Walker (1992)	functional type		
Faber (1991)*	league		
Barbault et al. (1991)*	functional analogue		

a context-specific simplification of the real world to deal with predictions of the dynamics of the systems or any of their components. We refer to 'organisms' to emphasize that the classification is not restricted to species but can apply to different phylogenetic levels and different life-history stages. A syndrome of environmental factors is a combination of biotic and abiotic processes that change as a result of a perturbation to the system, for example as a consequence of the passage of a fire. We also point out that similarity must be defined by the user in the context of the syndrome of environmental factors.

We further suggest that the term *response group* (or type) should be used to describe groups of organisms based simply on their behaviour in response to a particular perturbation and the term *functional group* be confined to groups where the response is mediated through the same mechanism.

GCTE and functional types

Given that GCTE wants to predict the response of functional types (FTs) under a wide range of environmental syndromes, then it has to seek a grouping of species that obeys the following mathematical relation:

$$\int(\{x_1 + x_2 + x_3\}, \{x_4 + x_5\}, \ldots \{\ldots + x_n\}, E) \approx \int(x_1, x_2, x_3, x_4, \ldots x_n, E)$$

where the x_i are species (taxa), the {bracketed} x_i are functional types, and E is the residual biotic and abiotic environment not incorporated in the x_i. Thus GCTE's interest in functional types is pragmatic. It needs a simplification tool, as originally suggested by Botkin. GCTE also requires that this equation apply not only to current combinations of x_i, but to future combinations and, more importantly, to new environmental scenarios, E.

Thus, GCTE requires a strong extrapolative property of its functional classification and thus seeks functional groups as defined above (see Tables 1.1 and 1.2). However, in terms of the papers in this volume most authors, except for Scholes, have used the 'functional type' in the sense of our structural guilds (see Table 1.1), without considering the response of the organisms involved.

What is the relationship between guilds, response groups and functional groups as we have defined them? If two species are in the same structural guild they use the same resource but in a different way and there is no *a priori* reason to expect them to respond to a perturbation in a similar way. Similarly, the observation that two species are in the same response group conveys no information about the mechanisms leading to the response and

thus no information about whether they might be in the same guild. However, if two species are in the same functional guild, they use the same resources in the same way, and thus it is more likely that they will respond to a perturbation in a similar way and therefore fall within the same response group and possibly the same functional group.

How can we recognize functional types?

There are three main approaches that have been used to identify functional types and guilds: we will call them subjective, deductive and data-defined (a form of pattern analysis).

A subjective approach is based on observations of one or more ecosystems in which it is taken for granted that functional types exist and that these can be defined inductively. Most ecological writing, as with most of our everyday description of our biological environment, is based on such groups (e.g. trees and shrubs, tree feeders, etc.). Various workers have used such a classification for wide-ranging groups of organisms. Examples of these include the work of Baker (1971), MacMahon (1976), Mannan *et al.* (1984), De Graaf *et al.* (1985), Shorrocks & Rosewell (1986), Adserson (1988), DuBowy (1988), Rader & Ward (1988), Wilson (1989), Croonquist & Brooks (1991), Faber (1991), Simberloff & Dayan (1991) and Root & Cappuccino (1992).

Some very comprehensive subjective, and mostly untested, classifications have been proposed. Examples include those of Johnson (1981), Verner (1984) and Newsome & Noble (1986). Johnson has attempted a classification of terrestrial vegetation of the USA for environmental impact assessment. He defined 95 hierarchically arranged guilds, based on dispersal, establishment and growth characters. The main purpose was to provide a non-subjective classification suitable for use by non-specialists. Verner (1984) produced an inductive two-dimensional classification of nesting and feeding zones of forest birds for management purposes. Newsome & Noble (1986) classified 86 weed species by multivariate techniques using 17 traits. They then compared the classes found in this way with subjective classes defined for invasive birds and described four groups applicable to both.

In a deductive approach, such as that of Noble & Slatyer (1980), van der Valk (1981), Huston & Smith (1987), Keddy (1992) and Scholes *et al.* (Chapter 13, this volume), a functional classification is derived from an *a priori* statement (or model) of the importance of particular processes or properties in the functioning of an ecosystem. The feasible set of functional categories are then deduced from these premises. The keystone species

classification of Paine (1980) can also be considered to be such an approach. The proposal by Walker (Chapter 5, this volume) is also a deductive approach based on assumptions about which characters might be most important in terms of climate change and can be obtained at a global scale. This is the most direct way of achieving a functional classification for a specific purpose; however, it is not clear whether it will lead to a workable number of functional types.

A data-defined approach uses multivariate techniques to seek clusters of species based on a set of characters. Again this has been used for a wide range of organisms. Examples include the work of Hagmeier & Dexter Stults (1964), Crome (1978), Holmes *et al.* (1978), Landres & MacMahon (1980), Pianka (1980), Folse (1981), Joern & Lawlor (1981), Bowers & Brown (1982), Newsome & Noble (1986), Niemi (1985), Szaro (1986), Cornell & Kahn (1989), Hawkins & MacMahon (1989), Jaksic & Medel (1990), Keddy (1990), Maddox & Root (1990), Winemiller & Pianka (1990), Finch (1991), Simberloff & Dayan (1991) and Leishman & Westoby (1992). In most cases the analyses are based on morphological and growth characters and might best be described as searching for a set of character syndromes (Stebbins 1974) or strategies (Grime *et al.* 1988). Thus, with respect to functional types, they are usually based on a set of characters that are surrogates for the response data. We discuss this point later in this chapter.

The three approaches can be used at different scales. The subjective and deductive classifications can be applied at local to global scales. The data-defined approach is appropriate to the local or regional scale and is unlikely to be used at the global scale because it would be difficult to gather appropriate data sets. There is also the question of whether the species properties and thus the functional types are discrete or continuous. If they are continuous then the data-defined approach would not produce clear groups and there will also be difficulty with a subjective approach. We discuss the general questions that can be raised with regards to this elsewhere (Noble & Gitay 1995).

Formal tests of functional classifications

One of the commonest approaches in attempting to find guilds or functional types has been to use multivariate analysis of character sets describing a set of species. This approach may not be suitable to the goals of GCTE as the detailed information required for each of the species to produce a classification may not be achievable even at a regional scale. It may be that a deductive approach is more appropriate for GCTE's objectives. However,

since the data-defined approach has been popular and some see the quantitative methodology as providing a sense of objectivity, despite the subjectivity in choosing character sets, distance or similarity measures and linkage methods, we will now consider the likely problems with the data-defined approach in producing a functional classification.

Functional classifications assume that there is an inherent structure in the world and that guilds and functional types are a revelation of that structure. Is this the case, and if it is, then how do we find that structure? If we fail to find consistent structure, does this imply that it does not exist, or is it a problem of inadequate selection of characters or inappropriate analytical techniques?

Ideally, a functional classification should be applicable to that suite of species wherever they occur and under a prescribed, but wide, range of environmental conditions and perturbations. Realistically, we might expect that classifications will vary in their robustness. Here we present a formal ranking of the degrees of robustness and then examine the performance of some existing classifications. We assume the following scenario.

- That we have collected data for a given pool of organisms. These data might include any characters or properties that reflect the function of the organisms in an ecosystem or their responses to perturbations.
- That we have also independently collected the data set at several different times and/or in several different locations; i.e. we have replicates of the data set.
- That several different researchers have been involved, each with the same purpose of the classification in mind, but each having collected different suites of characters that describe these organisms.
- That other researchers have also described the same pool of organisms, but this time with a different purpose in mind in seeking a functional classification.

We could analyse these data sets in several ways, and recognize the following outcomes.

1. *Uniqueness*: when similar classifications of a given data set are achieved by using *different analytical techniques*.
2. *Repeatability*: when similar classifications are achieved by using the same character sets collected at *different sites or different times*. By implication, character syndromes exist.
3. *Congruency*: when similar classifications are achieved by using *different character sets*, i.e. there are correlations between character syndromes. A hypothetical example is given in Table 1.3.
4. *Convergence*: when similar classifications of a pool of organisms are

Table 1.3 *Possible distribution of characters in organisms that would result in congruency*

The rows represent taxa and the columns characters. The taxa can be grouped based on the first five characters, which represent two character syndromes. They can also be grouped on the remaining six characters, which represent another two character syndromes. In this case the groupings of the taxa are identical and thus the classifications are congruent.

Characters

achieved by using data collected and analysed for *different purposes*. This implies that there is a limited number of feasible suites of physiological and life-history characters that must cover responses to all environmental syndromes; for example, groups with a similar response to drought will have a similar response to fire.

Some test results

Uniqueness

Anyone with experience of using multivariate techniques knows that different results can be obtained by using different similarity indices and linkage methods, and so this will not be discussed further. However, if classifications are to be compared, then it is important that the analytical techniques should be as similar as possible to ensure that any difference in the outcome reflects biological differences and not analytical ones.

Repeatability

We found some examples in the literature which can be used to test the criterion of repeatability. Friedel *et al.* (1988) gathered data sets on plants from two semi-arid sites. A cluster analysis produced ecologically interpretable groups, but the structure of the dendrogram was different (as illustrated in Fig. 1.1), although some of the groups were the same, implying that there is some repeatability.

Joern & Lawlor (1981) obtained a diet list of grasshoppers at several sites and concluded that there is reasonable agreement between the groups derived from their data. We have reanalysed one pair of their sites with 75% species overlap using a χ^2 test and found a significant repeatability of the groups ($p = 0.01$).

Szaro (1986) tested Verner's (1984) classification by counting bird densities in defined habitats in ponderosa pine forests eight times per year for three years. He found no consistent patterns in the variation of densities of individual species within a guild compared with the overall density of that guild. When he clustered species based on their density variation between habitats he found a different number of clusters in each of the three years with little consistency in the membership of the groups.
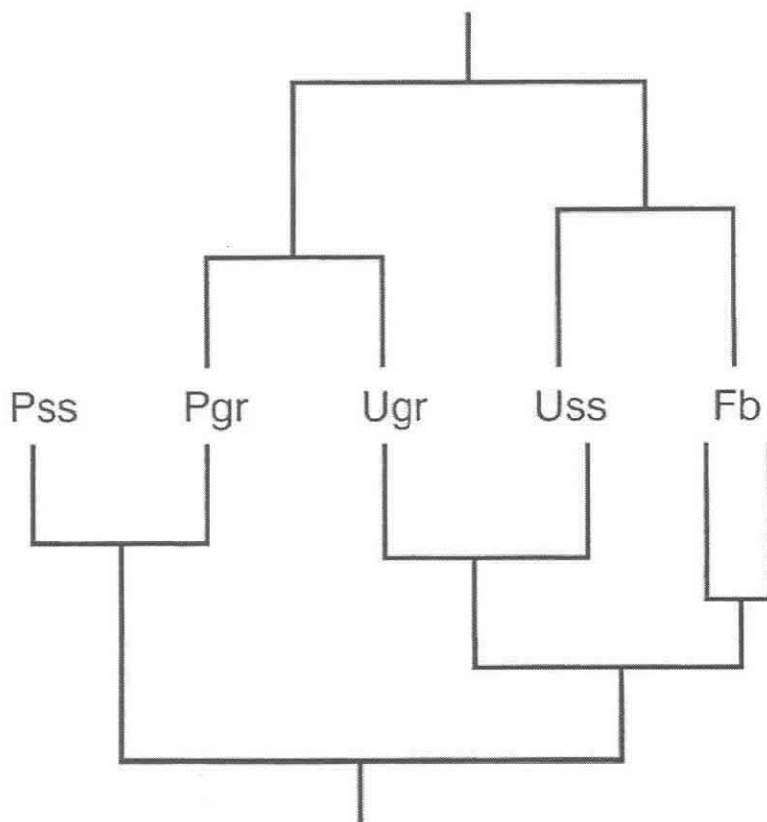

Figure 1.1   *The clusters derived by Friedel* et al. *(1988). Fb, forbs; Pss, palatable subshrubs; Pgr, palatable grasses; Ugr, unpalatable grasses; Uss, unpalatable subshrubs.*

Congruency and convergence

Grime *et al.* (1988) measured two data sets based on characters describing the regenerative and established phases of the same suite of plant species. The established phase showed three groups (reflecting mostly life history and life form), and the regenerative phase showed ten groups with no simple ecological (or phylogenetic) interpretation. The congruency between the classifications appears to be low. Shipley *et al.* (1989) collected morphological data for two life stages, juvenile and adult, where the characters were selected to reflect an adaptive syndrome to contrasting shore conditions. They found no association between the syndromes based on juvenile and adult life stages.

Joern & Lawlor (1981) used data sets based on diet characters and micro-habitat variables to classify grasshoppers. They concluded that there is a reasonable degree of agreement between the groups; this is supported by our reanalysis of their data using a χ^2 test in which we found that there was almost a significant level of congruency ($p = 0.06$).

We have analysed two data sets for rainforest species in Queensland, Australia (H. Gitay & I. R. Noble, unpublished), one representing morphological and life-history traits and the other representing the dynamic behaviour of the species over 30 years of observation made by J. H. Connell and others (Connell *et al.* 1984). We found that there was no relationship between the cluster membership in the two classifications (see Table 1.4). Thus there was no congruency.

We have found no suitable data sets in the literature to test for convergence.

In summary, there is some evidence of repeatability but little evidence of congruency, except within a restricted taxon (see Table 1.5) and we have not come across any data to test for convergence. We conclude that it is feasible to group species based on character syndromes (Stebbins 1974) and that these groupings are repeatable to some extent when based on the same character set measured in different locations or different times. There appears to be little evidence of congruency of the groups based on different character syndromes, such as groups based on juvenile and adult traits.

Tests of the utility of functional classifications

Few specific tests of the utility of functional classifications exist. Mannan *et al.* (1984) defined *a priori* members of bird guilds and found that these guilds did not respond consistently to a series of forest perturbations. They concluded that more guild categories were needed, approaching a species classification. Szaro (1986) also found that individual species within *a priori* defined guilds responded inconsistently between forest treatments.

Table 1.4 *A comparison of the congruency between classifications based on morphological and dynamic character sets*

Information statistics = 100.00, 56 d.f., $p \approx 0.55$.

Morphology	Dynamic								Total
	1	2	3	4	5	6	7	8	
2	1	3	0	0	0	1	0	1	6
3	0	1	0	1	1	1	0	1	5
4	5	4	0	0	1	1	0	0	11
5	0	2	0	0	1	0	0	0	3
6	1	2	1	1	1	0	0	0	6
7	3	5	1	2	0	0	0	0	11
8	1	1	0	0	1	0	1	0	4
9	1	0	0	0	2	0	0	0	3
10	0	0	0	0	1	0	0	0	1
Total	12	18	2	4	8	3	1	2	50

Source: H. Gitay & I. R. Noble, unpublished.

Sale & Guy (1992) observed that species assemblages of tropical fish are highly variable. Classifying the fish into subjectively defined guilds reduced the variability, but no more than with a null classification. They concluded that there is no evidence of an underlying organization of these assemblages at the guild level.

Against these three direct tests of functional classifications we must set the many examples where users have found classifications (usually subjective) to be satisfactory for their purposes (e.g. Diamond 1975, Noble & Slatyer 1980, Johnson 1981, Verner 1984, Keddy 1992, and many other modellers).

Conclusion

The use of the terms *guilds* and *functional types* has been inconsistent and has become confusing. We suggest that the term guild be used for classifications based on whether species use the same resources, and functional groups for classifications based on whether species respond in a similar way to a specified perturbation. Thus, functional types are a context dependent classification. For the purposes of GCTE, there is a more severe constraint since, in addition to being a means of simplification of the system that

Table 1.5 *Summary of case studies testing repeatability and congruency*

The table shows the result of the test, whether different life forms were incorporated in the range of organisms used in the analysis, whether a restricted range of taxa were included, and whether contrasting habitats were used.

Author	Test	Result a success?	Different life forms	Restricted taxa	Habitat contrast	Organisms
Friedel *et al.* (1988)	Repeatability, site	?Yes	Yes	No	?	Semi-arid plants
Joern & Lawlor (1981)	Repeatability, site	Yes	No	Yes	No	Grasshoppers
Szaro (1986)	Repeatability, time	No	Yes	No	No	Birds
Joern & Lawlor (1981)	Congruency	?Yes	No	Yes	No	Grasshoppers
H. Gitay & I. R. Noble (unpublished)	Congruency	No	No	No	No	Rainforest trees
Grime *et al.* (1988)	Congruency	No	Yes	No	?	Various UK plants
Shipley *et al.* (1989)	Congruency	No	Yes	No	Yes	Shoreline plants

describes similarity in responses to perturbations, the responses should also be due to the same mechanism if extrapolations to new circumstances are likely to be valid.

There is no doubt as to the utility of the concept of functional classifications, but as suggested by Hawkins & MacMahon (1989) and Landres (1983), this does not mean that functional groups exist. Unlike Heal & Grime (1991), we doubt that there is 'a universal [functional] classification of organisms in an ecosystem' since context is important. However, it is likely that functional types can be defined for specific purposes.

There has been some success in developing functional classifications that lead to ecologically interpretable groups. However, many classifications do not seem to get past the empirically obvious morphological and life-history-based groups. When we apply formal tests of robustness to the functional classifications of past work, we find some evidence that classifications are repeatable in space and time but little evidence of congruency: classifications carried out for the same purpose but with different character sets result in different groups and thus do not support the existence of an inherent structure in communities.

The apparent lack of congruency is a major warning of the difficulties still facing us in defining functional types on a broad scale. It is also important to know whether we seek a structural guild type of classification, where we are only interested in the resource use, or whether we want a classification based on the response of the species to perturbations (response groups) and have extrapolative power as GCTE will require (functional groups).

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